Monograph of the Gonostomatidae and Kahliellidae (Ciliophora, Hypotricha)
MONOGRAPH OF THE GONOSTOMATIDAE
AND
KAHLIELLIDAE
(CILIOPHORA, HYPOTRICHA)
Aims and Scope

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Monograph of the Gonostomatidae and Kahliellidae (Ciliophora, Hypotricha)

by

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Springer
Dedication

This book is dedicated to my friend and colleague Weibo Song from the Ocean University of China (OUC; Qingdao, China). Weibo made the OUC to an acknowledged centre of ciliate taxonomy and is author of many important works on the systematics of hypotrichs, especially from marine habitats.
Preface

The present book is part four of the Monograph of the Hypotricha, a series which reviews in great detail this highly interesting group of spirotrichous ciliates. The monograph is the most extensive revision since Kahl (1932), which is still an important treatise. The series will comprise six volumes.

The first volume is about the oxytrichids, a group which was considered for a long time as monophyletic because of the rather stable pattern of 18 frontal-ventral-transverse cirri (Berger & Foissner 1997, Berger 1999). However, the many molecular analyses published in the last decade combined with the sifting of the morphological and ontogenetic data indicate that this conspicuous pattern very likely already evolved in the last common ancestor of the Hypotricha so that it cannot be used as apomorphy of a subgroup of the hypotrichs (Berger 2006a, 2008). Now, I consider the fragmentation of dorsal kinety 3 as main morphological apomorphy of the oxytrichids (Berger 2006, p. 33; 2008, p. 46). Consequently, “18-cirri hypotrichs” which lack this fragmentation are very likely misplaced in the oxytrichids, for example, Gonostomum, Urosoma, Urosomoida, or some Oxytricha species (e.g., O. lanceolata). The misplacement of Gonostomum in the oxytrichids is also shown by molecular data, indicating that the dorsal infraciliature is as important as the ventral cirral pattern for the estimation of the major phylogenetic relationships within the hypotrichs.

The second volume of the series is mainly about the Urostyloidea (Berger 2006a), a rather large group whose members have the urostyloid midventral complex (zigzagging frontoventral cirri originating from more than six anlagen) in combination with the simple, plesiomorphic dorsal kinety pattern composed primarily of three bipolar bristle rows. Thus, species which also have a zigzagging cirral pattern, but a more complex dorsal infraciliature (e.g., dorsal kinety 3 fragmentation and/or dorsomarginal kineties) have been removed from the urostyloids, for example, Neokeronopsis and Uroleptus. The latter genus is now assigned to the so-called Dorsomarginalia (Berger 2006a), where it branches off rather basally. By contrast, Neokeronopsis belongs to the oxytrichids – a large subgroup of the Dorsomarginalia – because it has the same type of dorsal kinety fragmentation (Berger 2006a, p. 1190). This hypothesis was later corroborated by molecular data (Foissner & Stoeck 2008).

The Amphisiellidae and Trachelostylidae are the major taxa treated in the third volume (Berger 2008). The amphisiellids (e.g., Amphisiella, Lamrostyla, Hemisin-cirra) are non-dorsomarginalian hypotrichs with a more or less prominent frontoventral row formed from two or three anlagen, while the trachelostylids are a small group of marine 18-cirri hypotrichs with a curious dorsal kinety pattern, at least in the type species of the whole group. In addition, several genera of uncertain or unknown position within the hypotrichs have been included, for example, Apourosomoida, Erimophrya, or Hemiurosoma. Two species previously classified in Hemisin-
cirra have been transferred to the urostyloid genus *Anteholosticha* for which a new key was added.

The present volume is about the Gonostomatidae and the Kahliliellidae. *Gonostomum*, the name-bearing type genus of the Gonostomatidae, was previously assigned to the oxytrichids because the type species *G. affine* is basically an 18-cirri hypotrich (Berger & Foissner 1997, Berger 1999, see also second paragraph of present preface). We hypothesised that the simple dorsal kinety pattern – three bipolar kineties with caudal cirri – has evolved from the complex oxytrichid pattern by a loss of both dorsal kinety fragmentation and dorsomarginal kineties. Molecular analyses however indicated that *Gonostomum* branches off rather early in the Hypotricha tree. This supports the hypothesis that *Gonostomum* has taken over the simple dorsal kinety pattern from the last common ancestor of the hypotrichs (Berger 2008, p. 23). An important morphological apomorphy of the gonostomatids is the conspicuous oral apparatus: the major portion of the adoral zone extends mainly along the left body margin while the proximal portion curves knee-shaped towards cell midline. In addition, the paroral is composed of few to very few, rather widely spaced cilia. This pattern also occurs in some other genera, for example, *Paragonostomum*, *Wallackia*, and *Cladotricha* so that the reactivation of the Gonostomatidae Small & Lynn, 1985 seems useful. Further studies will show whether or not this was an equitable decision.

The kahliliellids are a difficult, uncertain group because a strong apomorphy is lacking. Currently, the preservation of parental structures (e.g., marginal rows, dorsal kineties) in the next generations is used as unifying feature. In addition, the type species of the whole group is relatively little known so that the present review is certainly only an interim solution. Molecular data about “kahliellid” species are rare and do not support, as in many other cases, the morphological classification.

Most taxa reviewed in the present book are terrestrial and/or limnetic, that is, very few (e.g., *Pseudokahliella marina*) are marine. Only few species, for example the very common and widely distributed *Gonostomum affine*, are known for a long time (Stein 1859). Most have been discovered in the 1900s by Kahl, Horváth, Ruinen, Foissner, and Eigner. Thirty-three gonostomatids, 15 kahliliellids, and 24 “other” species are reviewed as valid in the present volume. Details about synonymy rates will be provided in the last volume of the monographic series.

As in the previous volumes, almost all available data on morphology, ontogenesis, molecular biology, ecology, and faunistics have been included. For each species, a detailed list of synonyms is provided, followed by a nomenclature section. In the remarks, all important data concerning systematics, synonymy, phylogeny, and similar taxa are discussed. The morphology section contains a thorough description, following the same sequence in every species. If the data on various populations or synonyms do not agree very well, then they are kept separate so that even workers who do not agree with the synonymy proposed can use the revision. For several species, cell division data are available. They are also included because the ontogenesis is often very important to understand the interphasic cirral pattern correctly. The oc-
currence and ecology section contains a description of the type locality and all other localities where a species was recorded. In addition, almost all illustrations published so far have been included. Thus, with the present book the general microscopist need not refer back to the widely scattered original literature. Specialists, however, should always check both the present treatise and the original description or authoritative redescription when redescribing a known species.

The next major group which will be treated is the renowned, but difficult genus Uroleptus. As already mentioned above, Uroleptus has been assigned to the urostyloids previously because both have zigzagging ventral cirri. However, they differ distinctly in the dorsal kinety pattern (dorsomarginal row present vs. absent) and the gene sequences, indicating a convergent evolution of the so-called midventral pattern. Only recently, Foissner & Stoeck (2008) established the Uroleptidae, which comprise mainly limnetic and terrestrial species. Probably, volume 5 will also contain the Keronopsidae, a relatively small group characterised, inter alia, by a dividing cyst.

As already discussed in the preface to the amphisiellids and trachelostyliids, I will certainly find already known species which should have been reviewed in a previous volume. Such taxa will be treated in supplements at the end of each book, as already done in Berger (2006a, 2008) and the present revision (Apourosomoida). The last volume of the monographic series will contain a key and a systematic index to all species so that the user can find all hypotrichs very easily within the various volumes.

The Republic of Austria generously supported the monographic series via the Austrian Science Fund FWF and the Austrian Academy of Sciences, and I hope so that this will continue until the series is completed, in spite of the banking crisis.

Salzburg, August 2010

Helmut Berger
Acknowledgements and Permissions

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A General Section

The following chapters deal with the general external and internal morphology of the Gonostomatidae (= gonostomatids)\(^1\) and the Kahliellidae (= kahliellids), and terms specific to these taxa are described and explained. For general terms see also the corresponding sections of the previous volumes (Berger 1999, 2006a, 2008), especially Fig. 6a, b in Berger (1999), Fig. 1c, d, f, g in Berger (2006a), and Fig. 1a–h, 7a, b in Berger (2008). However, the illustrations of the individual species described in the systematic section are labelled in great detail so that even inexperienced workers will understand the morphology easily in most cases. For explanation of other terms, see Corliss (1979), Corliss & Lom (1985, 2002), Lynn & Corliss (1991), Hausmann & Bradbury (1996), Hausmann & Hülsmann (1996, 1996a), Hausmann et al. (2003), Fokin (2007), and Lynn (2008). The (supposed) ground pattern of the Hypotricha is discussed in detail in the phylogeny chapter of Berger (2008, p. 23). For comments on the ground pattern of the kahliellids and gonostomatids see the systematic section. Other topics, namely phylogeny, previous classifications, parasitism, ecology and distribution, and methods, are briefly discussed in chapters 2 to 6. In chapter 7 the applied species concept is briefly discussed and the nomenclatural acts are summarised.

1 Morphology, Biology, and Terminology

1.1 Size and Shape

Gonostomatids and kahliellids are usually moderately small or medium-sized, that is, the majority of the species is between 60 µm and about 200 µm long. The largest species treated in the present volume are Circinella arenicola (200–600 × 18–30 µm), Saudithrix terricola (200–350 × 70–150 µm), and Engelmanniella mobilis (170 to 270 × 18–23 µm). The smallest species is likely Paragonostomum minuta (about 33 × 12 µm in protargol preparations). The ratio of body length to body width ranges from about 2–3:1 (e.g., Kahliella, Parakahliella, Pseudokahliella; e.g., Fig. 65a, 110a) to about 15–17:1 in Circinella in protargol preparations (e.g., Fig. 57o), that is, in life such slender species have a ratio of up to 20:1. Thus, the body outline ranges from elliptical to worm-like. The ventral side of most species is, as in the vast majority of the hypotrichs, flat, the dorsal side more or less distinctly vaulted; however, some have an almost circular cross-section (e.g., Fig. 86i, 90a). The body is flexible (supple) and usually acontractile or only slightly contractile. No species with a truly rigid body is described. In the Hypotricha, a rigid cortex/body is only known from the Stylonychinae, a subgroup of the oxytrichids (for review, see Berger 1999, p. 499), and some species of uncertain phylogenetic position, for ex-

\(^{1}\) For names of higher taxa used in this book, see Fig. 6a, 9a and Table 3 in volume 3 (Berger 2008).
ample, *Rigidothrix* Foissner & Stoeck, 2006a or *Urospinula* Corliss, 1960 (Foissner 1983). The adoral zone of membranelles, the most prominent part of the oral apparatus, is in the left anterior body portion and usually occupies about 30–35% of body length, in some gonostomatids up to 50%. For some general terms used in the descriptions, see Fig. 1a–c.
1.2 Nuclear Apparatus

The species reviewed in the present book have an ordinary nuclear apparatus, that is, two or several macronuclear nodules and one or more micronuclei (Fig. 1a, Table 1). *Circinella* species have many (up to about 100) small macronuclear nodules (e.g., Fig. 57q) and for few species a single macronucleus is described (Table 1). Usually, the nuclear apparatus is somewhat left of or in body midline (e.g., Fig. 1a, 3a, 4b). As in other ciliate species, the nuclear pattern is very important for species identification. It is usually easily recognisable in life with differential interference microscopy, after staining with methyl-green pyronin, or after protargol impregnation (e.g., Fig. 24b).

The macronucleus is – as in most other ciliates – homomerous and polyploid. Homomerous means that there is no distinct differentiation into DNA-rich and DNA-poor parts, as is the case in the heteromerous macronuclei characterising groups like the Chlamydodontidae and Dysteriidae (Raikov 1969). For detailed reviews on the nuclear apparatus of hypotrichs and ciliates in general, see Raikov (1969, 1982, 1996), Klobutcher & Prescott (1986), Hoffman et al. (1995), Prescott (1994, 1998), and Bleyman (1996).

The development of the gonostomatid and kahliellid nuclear apparatus during cell division is the same as in many other hypotrichs. The micronuclei divide mitotically, whereas the fused macronucleus makes one or more rapid, successive amitotic divisions to produce the species-specific number of nodules in each filial product (Prescott 1994). Of course, the macronuclear nodules of the hypotrichs treated possess a replication band, a feature which evolved in the stem-line of the spirotrichs (e.g., Adl et al. 2005, Lynn 2008); for details on this feature see Olins & Olins (1994). For documentation of the division of the nuclear apparatus in gonostomatids and kahliellids, see, for example, *Gonostomum algicola* (Fig. 18c, p, 19b, h, j, l, n, p, r, t), *Kahlia simplex* (Fig. 67i–r, t–z, 68a–e, 70c, f, j), or *Engelmanniella mobilis* (Fig. 89c, g, i, j, l–n, q).

1.3 Contractile Vacuole and Cytopyge

The contractile vacuole is involved in osmoregulation to prevent a disruption of the cell due to the continuous influx of water into the ciliate. The influx occurs according to the osmotic gradient between the cytoplasm and the surrounding medium (Paulin 1996). The contractile vacuole of the taxa treated in the current volume is, as is usual for the hypotrichs, near the left cell margin at about 40–50% of body length or somewhat ahead of it; usually it is not ahead of the level of the proximal end of the adoral zone of membranelles (Fig. 1c, 2b). In some species (e.g., *Paragonostomum* spp., *Wallackia* spp.) it is somewhat displaced inwards (e.g., Fig. 33a, b, 104c), and in *Stenotricha arenicola* it is at about 60% of body length, that is, distinctly behind mid-body (Fig. 111b). Several species have more or less distinct col-
Table 1 Nuclear apparatus of gonostomatid and kahliellid ciliates and other species reviewed in this monograph

<table>
<thead>
<tr>
<th>Nuclear apparatus</th>
<th>Species a</th>
</tr>
</thead>
<tbody>
<tr>
<td>One macronucleus</td>
<td>Cladotricha koltzowii (Fig. 43a); Orthoamphisiella breviserises (Fig. 107a, e, g, i, j); Strongyldium packii (Fig. 50a)</td>
</tr>
<tr>
<td>Two macronuclear nodules; two or more micronuclei or number of micronuclei not known</td>
<td>Afrokahliella binucleata (Fig. 79a, f, h, i); Afrokahliella namibicola b (Fig. 76a, i); Apourosomoida kahlí (Fig. 113a); Apourosomoida variabilis (Fig. 114h); Cladotricha koltzowii (Fig. 43j); Cladotricha sagitata (Fig. 44a); Cladotricha sigmoidea (Fig. 45a–c); Cladotricha sp. (Fig. 46a, b, 47a, b); Deviata abbrevescens (Fig. 96a, b, h); Deviata bacilliformis (Fig. 98b); Deviata estevesii (Fig. 104b, h); Gonostomum affine (Fig. 10a, b); Gonostomum gonostomoidum (Fig. 25b); Gonostomum namibiense (Fig. 22a, e, g, i); Gonostomum sp. (Fig. 27a, c); Gonostomum strenum (Fig. 23a, e); Gonostomum terrestre (Fig. 26a, b); Kahliella acrobates (Fig. 62c); Kahliella simplex (Fig. 65g); Neogeneia costata (Fig. 85a, b); Neogeneia horcutialis (Fig. 84a, c); Neowallackia petegofii (Fig. 55b); Orthoamphisiella grelli (Fig. 106a); Paragonostomum binucleatum (Fig. 35a, e, g); Paragonostomum caudatum (Fig. 30a, h, j); Paragonostomum rarisetum (Fig. 32a); Perisincirra kahli (Fig. 81a); Perisincirra longicirrata (Fig. 83a, e); Saudithrix terricola b (Fig. 108a, g); Strongyldium packii (Fig. 50a); Trachelochaeta bryophila (Fig. 56a); Urosona macrostomum (Fig. 28a); Wallackia bujoreani (Fig. 40a, d); Wallackia elegans (Fig. 42a, c); Wallackia schiffmanni (Fig. 39a)</td>
</tr>
<tr>
<td>Two macronuclear nodules and one micronucleus in between</td>
<td>Apourosomoida elongata (Fig. 112a); Perisincirra paucicirrata (Fig. 82d, f)</td>
</tr>
<tr>
<td>Four macronuclear nodules (in some species the nodules are arranged in pairs)</td>
<td>Afrokahliella halophila a (Fig. 77a, n, p, r, t); Afrokahliella namibicola a (Fig. 114a); Cladotricha koltzowii (Fig. 43k–m); Deviata bacilliformis (Fig. 98a, c, n); Deviata brasilienis (Fig. 100b); Deviata polycirrata (Fig. 102a, c); Deviata quadrinucleata (Fig. 99a, b); Deviata spirostoma (Fig. 101b); Fragmocirrus espeletiae a (Fig. 80a, g); Gonostomum albicarpathicum a (Fig. 21a, c); Orthoamphisiella stramenticola (Fig. 105a, j); Stenotricha arenicola a (Fig. 111b, d)</td>
</tr>
<tr>
<td>Five to eight, usually eight macronuclear nodules</td>
<td>Engelmanniella mobili s (Fig. 86d, 87e); Paragonostomum minuta (Fig. 38c); Paragonostomum multinucleatum a (Fig. 33a, d, f, i, j); Parakahliella haideri (Fig. 75a, e); Parakahliella macrostoma (Fig. 73g); Parakahliella terricola (Fig. 74b)</td>
</tr>
<tr>
<td>More than eight macronuclear nodules</td>
<td>Circinella arenicola (Fig. 57a, q); Circinella filiformis (Fig. 61a, h); Circinella vettersii (Fig. 60a, f); Cladotricha australis (Fig. 48a, h); Cladotricha halophila (Fig. 49a, c); Deviata rositae (Fig. 103a–c); Engelmanniella mobilis a (Fig. 86k); Gonostomum kuehnelti (Fig. 15c; Fig. 123a, f in Berger 1999); Neowallackia franzi (Fig. 52a, e); Neowallackia ghangriai (Fig. 54c); Paragonostomum simplex (Fig. 36a); Parakahliella haideri (Fig. 75b); Parakahliella macrostoma (Fig. 73e); Pseudokahliella marina (Fig. 109a, g, 110i)</td>
</tr>
</tbody>
</table>

a For details on the nuclear apparatus, see individual descriptions.

b The number of macronuclear nodules varies from one to four.
lecting canals extending near the left body margin during diastole (e.g., Fig. 1c, 18a, 75c). Species living in highly saline habitats (*Cladotricha*, *Apourosomoida*) often lack a contractile vacuole. However, it is known that in halophile species the vacuole – if present at all – contracts in rather long intervals so that one cannot exclude that this organelle has sometimes been overlooked or misinterpreted as food vacuole. The excretory pore is, as in the other hypotrichs, on the dorsal side above the contractile vacuole (Fig. 88c).

Little is known about the cytopyge of the species treated in the present volume. Usually this organelle is located in the posterior body portion near the left cell margin (Fig. 52c).

1.4 Cytoplasm, Cortex, and Colouring

The cytoplasm of the gonostomatids, the kahlidiids, and the other species treated in the present book is more or less colourless and contains the ordinary inclusions, for example, greasily shining globules, rod- and/or Y-shaped cytoplasmic crystals, and food vacuoles. Some species have cortical granules (see chapter 1.5) while symbiotic algae are not described.

The cortex of the species reviewed here is supple, that is, the body is flexible when freely motile. Consequently, it is very unlikely that your specimen/population belongs to a species described in the present book if its body is rigid and moves like a board when freely swimming; if you find such a specimen/population you have to look at the styloonychines (Berger 1999, p. 499); only very view other hypotrichs, for example, *Rigidothrix goiseri*, have a rigid body (Foissner & Stoeck 2006a). The ultrastructure of *Engelmanniella mobilis*, a species (preliminary) classified in the kahlidiids was studied by Wirnsberger-Aescht et al. (1989), that of *Kahlidiella simplex* by Fleury et al. (1985, 1985a). Both species have a single layer of longitudinal microtubules underneath the somatic pellicle. Likely for that reason these and other
non-rigid species have a more or less flexible cortex. For details, see p. 367, 502 and individual papers.

1.5 Cortical Granules

Cortical granules occur in about 23% of the species reviewed (Table 2). Their size, shape, colour, and arrangement are very important features, which cannot usually be recognised after protargol impregnation. Consequently, live observation is absolutely necessary for a reliable identification of a hypotrich (e.g., Stein 1859, Kahl 1932, Borror & Wicklow 1983, Berger & Foissner 1987a, Foissner et al. 2002a, b). Note

<table>
<thead>
<tr>
<th>Species</th>
<th>Size (µm)</th>
<th>Shape</th>
<th>Colour</th>
<th>Arrangement and remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Afrokahlilella binucleata</td>
<td>1.0–1.3</td>
<td>globular</td>
<td>colourless</td>
<td>arranged in closely spaced, longitudinal rows; with central dark dot</td>
</tr>
<tr>
<td>Engelmanniella mobilis</td>
<td>0.5–1.0</td>
<td>globular</td>
<td>colourless to yellowish</td>
<td>arranged in about 17 longitudinal rows; very conspicuous at high magnification</td>
</tr>
<tr>
<td>Gonostomum affine</td>
<td>&lt;1.0</td>
<td>globular</td>
<td>colourless</td>
<td>loosely arranged in indistinct longitudinal rows</td>
</tr>
<tr>
<td>Gonostomum algicola</td>
<td>0.8 × 0.5</td>
<td>rod-shaped</td>
<td>colourless, stain red when MGP is added</td>
<td>loosely spaced in longitudinal rows</td>
</tr>
<tr>
<td>Gonostomum kuehnnelti</td>
<td>1.0–1.5</td>
<td>rod-shaped</td>
<td>colourless, stain red when MGP is added</td>
<td>loosely arranged</td>
</tr>
<tr>
<td>Gonostomum nambienne</td>
<td>1.0 × 0.3</td>
<td>rod-shaped</td>
<td>colourless, stain red when MGP is added</td>
<td>closely spaced</td>
</tr>
<tr>
<td>Gonostomum strenuum</td>
<td>1.0–1.2 × 0.6</td>
<td>ellipsoidal</td>
<td>colourless, stain red when MGP is added</td>
<td>arranged in loose rows, form distinct fringe</td>
</tr>
<tr>
<td>Kahlilella simplex</td>
<td>&gt;1.0</td>
<td>globular</td>
<td>colourless</td>
<td>arranged in loose rows</td>
</tr>
<tr>
<td>Neowallackia ghngriai</td>
<td>?</td>
<td>?</td>
<td>colourless</td>
<td>scanty dispersed; in addition to the cortical granules, extrusomes (1.6–2.1 × 0.6–0.7 µm after protargol impregnation, dispersed throughout body) are present</td>
</tr>
</tbody>
</table>
that the “correct” colour can only been seen at well-adjusted bright-field illumination; the presence or absence of cortical granules should be checked with differential interference contrast and by staining with methyl-green pyronin. For details on the ultrastructure of the cortical granules of *Engelmanniella mobilis*, see p. 502 (Wirnsberger-Aescht et al. 1989).

### 1.6 Movement

The species reviewed are – like the vast majority of the hypotrichs – usually thigmotactic, that is, they adhere more or less strongly to the substrate whenever the opportunity arises. They creep on their flattened ventral side by means of the cirri. Usually, the specimens move to and fro more or less hastily. All species have a supple body which bends to varying degrees. Thus, when you see a rigid, freely motile hypotrich you can exclude that it is treated in the present volume. No exhaustive stud-
ies on the movement of gonostomatids or kahliliellids exists. Tailed or slender species are sometimes attached to the substrate via a fine thread (Fig. 30g).

1.7 Somatic Ciliature and Ultrastructure

As is usual for hypotrichs, the somatic ciliature of the Gonostomatidae, Kahliliellidae, and the other taxa reviewed in the present book consists of rows and localised groups of cirri on the flattened ventral side, and several rows of more or less widely spaced, usually short (2–5 µm), stiff cilia (bristles) on the vaulted dorsal side (Fig. 1b). Many species have three dorsal kinetics, a feature of the ground pattern of the Hypotricha (Berger 2008, p. 28). Caudal cirri are, if present at all, part of the dorsal ciliature because formed at the end of bipolar kinetics (Fig. 1c, 2b). A “cirral row” in hypotrichs is either a true row (all cirri originate from the same anlage; e.g., marginal row), a pseudorow (cirri originate from different anlagen; e.g., transverse cirri), or a mixed row (two or more “true” rows form a row; mainly present in the amphisiellids; see p. 10 and Fig. 1d–f in Berger 2008 for detailed explanation).

The arrangement of cirri and dorsal kinetics is very important for the systematics. Consequently, as in other groups of hypotrichs, an unambiguous terminology is needed to describe and understand the morphology of the taxa treated (Fig. 1a–c, 2a, b, 3a, 4a, b). The paragraphs below describe the individual cirri and cirral groups. Many cirri of the various higher taxa of the hypotrichs (e.g., Urostyloidea, Oxytrichidae, Amphisiellidae, Trachelostylidae, Kahliliellidae, Gonostomatidae) can be homologised and therefore have, of course, the same designation in these taxa. A detailed discussion of the confusing terminology of some cirri is provided by Berger (1999, 2006a). As in the previous volumes (Berger 1999, 2006a, 2008), I use the well-established numbering system introduced by Wallengren (1900) to designate the individual cirri and/or cirral rows and the anlagen from which these cirri originate (Fig. 2a); however, note that this system was basically established to characterise the pattern of 18-cirri hypotrichs (Fig. 6a in Berger 1999). In the following, the cirral groups and structures are explained in the same sequence as they are usually treated in the individual species descriptions. More specific terms are explained at the individual descriptions of genera and species.

Frontal cirri (FC). These cirri are near the anterior end of the cell (e.g., Fig. 2a, 3a, 4a). All taxa discussed have – like the oxytrichids, amphisiellids, trachelostyliids, and many urostyliids – three more or less distinctly enlarged frontal cirri which usually form a slightly oblique pseudorow. In some gonostomatids the left cirrus is usually somewhat displaced posteriad and somewhat larger than the other two frontal cirri (e.g., Fig. 3a, 18b, 21f). The frontal cirri are undoubtedly homologous in all groups. The left one (= cirrus I/1) is usually ahead of the paroral. It is formed (in most cases) from the same anlage (= anlage I) as the undulating membranes. The middle cirrus is homologous to cirrus II/3 of, for example, the 18-cirri hypotrichs (Berger 1999). It is produced, like the buccal cirrus, from anlage II. The right frontal
Fig. 2a, b Schematic illustration (from Berger 2008) of the ventral and dorsal side of the supposed last common ancestor of the Hypotricha (Fig. 6a, square 9 and Fig. 9a, square 1 in Berger 2008). The 18 frontal-ventral-transverse cirri and the three caudal cirri are grey, the marginal cirri are black. Broken lines connect cirri which originate from the same frontal-ventral-transverse cirri anlage; dotted lines in (a) connect or surround cirral groups. Perhaps the three postoral ventral cirri have been right of the proximal portion of the adoral zone in the last common ancestor (dotted cirri). The dorsal kinety pattern of the ancestor was very likely rather simplex, that is, composed of three bipolar kineties each bearing a caudal cirrus. Detailed explanation of structures, see text; details about the phylogeny, see chapter 2 in Berger (2008).

AZM = adoral zone of membranelles, BC = buccal cirrus, CC = caudal cirri, CV = contractile vacuole, FC = frontal cirri, FVC = frontoventral cirri, LMR = left marginal row, PTVC = pretransverse ventral cirri, PVC = postoral ventral cirri, RMR = right marginal row, TC = transverse cirri, I–VI = frontal-ventral-transverse cirri anlagen, 1–4 = cirri within anlage (a), 1–3 = dorsal kineties (b).
cirrus (= cirrus III/3) is usually behind/close to the distal end of the adoral zone of membranelles.

**Buccal cirrus (BC).** This cirrus (= cirrus II/2) is usually right of the paroral (Fig. 2a, 3a, 4a); in some species it is ahead of the undulating membranes. For a discussion of the confusing terminology, see Berger & Foissner (1997) and Berger (1999). Most species reviewed in the present volume have one buccal cirrus which is certainly the plesiomorphic state. Few species, for example, *Neowallackia franzi* (Fig. 53a), *Saudithrix terricola* (Fig. 108f), or *Pseudokahliella marina* (Fig. 109f) have two or more buccal cirri. Usually, the buccal cirrus has an ordinary size, like, for example, the marginal cirri.

**Parabuccal cirrus/cirri (PC; cirrus III/2).** Usually, at least one parabuccal cirrus is present in the species treated in the current volume. Parabuccal cirrus is another designation for cirrus III/2, which is the cirrus behind the right frontal cirrus (Fig. 2a, 3a). In the 18-cirri hypotrichs, cirrus III/2 forms – together with cirri IV/3, VI/3, and VI/4 – the four frontoventral cirri (Fig. 2a, 36k; Fig. 6a in Berger 1999).

**Frontoventral cirri (FVC).** In 18-cirri hypotrichs (e.g., some *Gonostomum* species, Fig. 2a, 3a, 22e; Berger 1999) this group comprises four cirri (III/2, IV/3, VI/3, VI/4) between the anterior portion of the right marginal row and the paroral. They are arranged in various patterns, usually, however, in a V-shaped one (Berger 1999). Another term for the frontoventral cirri VI/3 and VI/4 is frontoterminal cirri (see next entry). When the number of cirri formed from the relevant anlagen is distinctly higher than one or two, then the species have frontoventral rows (see below).

**Frontoterminal cirri (FT).** This term was introduced by Hemberger (1982, p. 11) for the frontoventral cirri VI/3 and VI/4 (see previous entry) because they migrate to near the anterior body end in the middle and late phase of cell division (e.g., Fig. 36k). Borror & Wicklow (1983) thus designated these cirri, which never form primordia during morphogenesis, migratory cirri. In most species reviewed here not two, but more frontoterminal cirri are present, provided that anlage VI is available at all (Fig. 2a).

**Frontoventral row.** This is a general term for a cirral row formed from a frontal-ventral-transverse cirri anlage, usually anlage III (= parabuccal row), IV, V, or VI (Fig. 4a). Sometimes it is difficult to decide whether a row is a frontoventral row or a right marginal row. A relatively high number of species reviewed in the present volume lacks one anlage, respectively, the resulting frontoventral row. The genera and species treated have a rather different cirral pattern preventing a uniform designation of the individual structures, as, for example, in the 18-cirri hypotrichs. Nonetheless, I tried to apply a uniform terminology, as far as possible.

**Postoral ventral cirri (PVC).** In most 18-cirri hypotrichs this term is commonly used for the cirri IV/2, V/3, and V/4, which are behind the proximal end of the adoral zone (Fig. 2a). In *Gonostomum* species and some other taxa (trachelostylids, some *Lamtostyla*-species; Berger 2008), the postoral ventral cirri are displaced anteriad right of the proximal portion of the adoral zone of membranelles (e.g., Fig. 3a). Perhaps this is the older state within the hypotrichs (Berger 2008, p. 48).
Pretransverse ventral cirri (PTVC; PT in Berger 2006a). This term was introduced by Berger & Foissner (1997) for two cirri of 18-cirri hypotrichs (Fig. 2a). Accessory transverse cirri is an older, synonymous term introduced by Wicklow (1981, p. 348). They are usually arranged immediately ahead of the transverse cirri V/1 and VI/1 and are designated V/2 and VI/2 according to Wallengren’s scheme. The present volume treats only a limited number of species having pretransverse ventral cirri, for example Gonostomum namibiense (e.g., Fig. 22e). In species with a reduced number of pretransverse ventral and transverse cirri they are often difficult to distinguish because it is not known which cirri have been lost; in addition, the size of cirri of these two groups is often rather similar. In such cases, ontogenetic data are needed for a correct designation.

Transverse cirri (TC). These cirri, which often form a distinct pseudorow, are usually in the posterior quarter of the cell (e.g., Fig. 2a, 3a, 15a, 108f). Transverse cirri are part of the ground pattern of the Hypotricha (Berger 2008, p. 35) and therefore present in many hypotrichs. However, in most kahlidiellids and many gonostomo-
matids they are rather inconspicuous or even lacking (Fig. 3a, 4b). Further details, see Berger (2008, p. 16).

18-cirri hypotrich. The last common ancestor of the Hypotricha very likely had 18 frontal-ventral-transverse cirri arranged in a highly characteristic pattern originating from six (I–VI) anlagen (e.g., Fig. 2a; Fig. 6a in Berger 1999). Consequently, this pattern occurs at just about all sites of the Hypotricha tree. Previously I thought that this curious cirral pattern is an apomorphy of the oxytrichids (Berger & Foissner 1997, Berger 1999). By contrast, Eigner (1997, p. 553) and some other workers supposed that the 18 cirri have evolved several times independently. However, this is
almost impossible because the pattern, including its formation, is too complex to evolve convergently. Further details, see Berger (2008, p. 23).

**Marginal cirri (LMR, RMR).** These cirri run along the left and right body margin. Most hypotrichs have one left and one right marginal row (Fig. 2a, 3a, 4a, b). Marginal rows are true cirral rows because all cirri of each row originate from the same anlage. The right marginal row often commences near the distal end of the adoral zone; in some species it is distinctly shortened anteriorly or it extends onto the dorsolateral surface. The left row usually begins left of the proximal portion of the adoral zone. In most species the marginal rows are slightly shortened posteriorly, that is, they do not extend to the posterior tip of the cell so that the rows are distinctly separated. However, the gap between the rows is sometimes difficult to recognise because it is seemingly occupied by the caudal cirri, which, however, insert on the dorsal side. A rather high number of species reviewed in the present book has more than two marginal rows, for example, *Kahliaella* spp. (Fig. 4a, b), *Deviata* (Fig. 96g), *Fragmocirrus* (Fig. 80f), *Saudithrix* (Fig. 108f, h), or *Pseudokahliaella* (Fig. 109f). However, sometimes it is difficult to distinguish between frontoventral row and right marginal row. In some species the additional marginal rows are new rows, that is, they originate from a primordium (e.g., *Saudithrix*). In most species with more than two marginal rows, the additional rows are remnants of the parental or grand-parental generation (e.g., *Kahliaella* spp., *Engelmanniella*). This feature – its formation was termed neokinetal wave by Eigner (1995, p. 343) – is also known from other groups, for example, the stylonychine *Coniculostomum* (Kamra & Sapra 1990; for review, see Berger 1999, p. 606), showing that this relatively simple feature evolved convergently.

**Dorsal cilia (DB; 1, 2, 3, ...).** The dorsal side of all hypotrichs and euplotids is covered by a more or less high number of kineties, which are therefore named dorsal kineties or dorsal bristle rows (e.g., Fig. 1a–c, 2b). The gonostomatids have – like many urostyloids and amphisiellids – three bipolar kineties (Fig. 2b, 10j, 18c), which is likely the state in the stem line of the hypotrichs (Berger 2008, p. 28). Previously, that is, when I assigned *Gonostomum* to the Oxytrichidae (Berger 1999, p. 367), I hypothesised that this simple pattern (dorsomarginal kineties and fragmentation lacking) evolved from the *Oxytricha*-pattern (dorsomarginal kineties and kinety fragmentation present) via the *Urosomoida*-pattern (loss of kinety fragmentation). The kineties of the Gonostomatidae are basically bipolar, that is, they extend from

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*Fig. 4a, b* Infraiciature of ventral and dorsal side and nuclear apparatus of a typical kahliliellid (*Kahliaella simplex*; from Berger & Foissner 1987. Protargol impregnation). Arrowhead in (a) marks left frontal cirrus (= cirrus I/1). Arrows mark old cirral rows from previous generations with widely spaced cirri. The preservation of parental ciature is the main (relatively weak) feature of the kahliliellids (details see systematic section). The major differences to the gonostomatids (Fig. 3a, b) are the presence of a dorsomarginal kinety (kinety 4 in b) and the preservation of parental cirri. AZM = adoral zone of membranelles, CC = caudal cirri (= rear portion of dorsal kinety 1), LMR = left marginal row, MA = macronuclear nodule, MI = micronucleus, RMR = right marginal row, I–VI = frontoventral cirri rows (= cirri originating from anlagen I–VI), 1–4 = dorsal kineties. Description of species, see page 367.
near the anterior to near the posterior body end. Dorsomarginal kineties, which originate from/near the right marginal primordium, are present in the Kahliellidae, although this feature is not yet confirmed for the type species of *Kahliella*. Fragmenting kineties are lacking in all taxa reviewed in the present book. Fragmentation is characteristic for the oxytrichids (for review, see Berger 1999; 2006a, p. 1190) and few other taxa (e.g., *Trachelostyla pediculiformis*; Berger 2008, p. 478), whereas dorsomarginal kineties are probably the main morphological apomorphy of the Dorsomarginalia (Berger 2006a). The importance of the dorsal kinety pattern in elucidating the phylogeny of the hypotrichs has been underestimated for a long time (Foissner & Adam 1983a). Recent molecular studies largely support groups based on features of the dorsal kinety pattern. Its exact description is therefore an absolute prerequisite for a serious description and classification of a hypotrich. However, ontogenetic data are often needed to understand a pattern correctly, that is, to know whether or not dorsomarginal rows and/or kinety fragmentation are present.

**Caudal cirri (CC).** They originate at the posterior end of the bipolar dorsal kineties, that is, they are part of the dorsal infraciliature (Fig. 1c, 2b). Dorsomarginal kineties, present in most kahliellids but lacking in all other species reviewed in the present volume, are never associated with caudal cirri, that is, in the latter group (non-kahliellids) the number of caudal cirri (if present at all) is usually equal to the number of dorsal kineties, assuming that each kinety forms one cirrus. In *Parakahlilla* and *Afrokahlilla* only kineties 1 and 2 produce caudal cirri, sometimes however, up to 12 per row (Table 23). The caudal cirri are arranged dorsally, usually at or very close to the rear body end, frequently above the gap formed by the rear end of the marginal rows. Thus, live and silver preparations must be studied with high diligence to avoid a misinterpretation of caudal cirri as marginal or transverse cirri or vice versa. In vermiform species it is sometimes impossible to decide whether cirri at the rear cell end are caudal, transverse, or marginal cirri, even in protargol preparations. In such cases, ontogenetic data are indispensable for a correct interpretation. The caudal cirri of many species are rather inconspicuous, that is, neither very long and/or strong. In *Wallackia*, however, they are very prominent because they are long and look like Pasteur pipettes (Fig. 39a, d, 42I). The presence of caudal cirri is a plesiomorphy in the reviewed taxa because they are (very likely) already part of the ground pattern of the hypotrichs (Berger 2008, p. 35). Some taxa lack caudal cirri (e.g., *Engelmaniella*, *Neowallackia*). There is no doubt that the loss, a rather simple feature, occurred many times independently in the hypotrichs (Berger 1999, 2006a, 2008).

**Fine structure of cirri and membranelles.** Studies about this topic are rare. Fleury et al. (1985) investigated a *Kahlilla* species whereas Wirnsberger-Aescht et

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1 Note that the fragmentation present in *Aplyosomoida halophila* (Fig. 110q in Berger 2008) is very likely not homologous to the oxytrichid fragmentation.

2 For the determination of a hypotrich it is, however, often not necessary to know the dorsal kinety pattern exactly.
al. (1989) analysed the ultrastructure of *Engelmanniella mobilis*. For some details see the systematic section and the individual papers.

### 1.8 Oral Apparatus

The oral apparatus is composed, as in the other hypotrichs, of an adoral zone of membranelles, two undulating membranes (paroral and endoral), the buccal cavity (buccal field, oral field), and associated fibres including the cytopharynx. For a detailed characterisation and terminology of the various oral types present in the hypotrichs, see Berger & Foissner (1997), Berger (1999, 2006a, 2008), and Foissner & AL-Rasheid (2006). Detailed studies of the oral apparatus will provide further interesting differences among various taxa. However, these features are generally very sophisticated and at present known only for a very low number of species.

The adoral zone of membranelles extends from the anterior body end roughly along the left body margin to near midline of the cell and usually terminates at about 20–35% of body length. In some taxa, for example, *Circinella* and *Engelmanniella*, the adoral zone occupies only 6–16% of body length while it is very large (sometimes up to 50%) in *Pseudokahlillla* and some gonostomatids (e.g., Fig. 24a–d). In most hypotrichs it is more or less shaped like a question mark and the distal end does not extend far posteriorly, that is, the so-called DE-value\(^1\) is often less than 0.11 (Berger 2006a, p. 18). In the gonostomatids and in *Kahlillla* the shape of the zone is rather characteristic because the middle range extends along the left body margin while the proximal part bends knee-shaped towards the cell-midline (Fig. 3a, 4a). In addition, the relative length of the zone is often near 50% of body length, a value also known from the stylonychines (Berger & Foissner 1997, Berger 1999).

*Apourosomoida* species (p. 684) and other hypotrichs have a more or less distinct gap (break) in the adoral zone at the left anterior body corner (e.g., Fig. 114g; further examples see Berger 2006a, 2008). The anterior, often transversely arranged portion is termed distal, frontal, or collar portion and largely on the dorsal side of the frontal scutum, the anteriormost part of the body; the posterior part of the zone is termed proximal, ventral, or lapel portion. The membranelles of the species treated in the present volume very likely have the ordinary fine structure, that is, each membranelle is composed of (i) two long kineties, (ii) one moderately long kinety, and (iii) one short kinety. For details on the ultrastructure in *Kahlillla simplex* (p. 367) and *Engelmanniella mobilis* (p. 502), see Fleury et al. (1985) and Wirnsberger-Aescht et al. (1989).

Hypotrichs have two undulating membranes, the paroral and the endoral\(^2\) (e.g., Fig. 3a, 78a, 108m). For detailed discussion of various patterns formed by the mem-

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1. DE-value = distance DE divided by length of adoral zone of membranelles (Fig. 1a; Berger 2006a, 2008).
2. Note that the paroral and the endoral have been confounded sometimes (e.g., Wirnsberger-Aescht et al. 1989).